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Collembola in the biotopes of the Kampinos National Park distinguished according to the natural succession

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With 7 figures

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1. Introduction

The aim of the paper has been to describe the occurrence of Collembola in various biotopes of the Kampinos National Park (KNP), and an attempt is made to relate this occurrence to the directions of plant succession.

KNP is located to the north-west of Warsaw on a dune terrace 40 km long, and few to some scores km broad. On the entire area the primary substrate consists of river sands formed most probably during the Palaeolithic age (KOBENDZA 1930) in a pattern of parabolic dunes. The highest dune steps border the area to the north and south. The dune ridges cause a higher relative level of ground waters, which fill the depressions between the dunes (TRACZYK, H., and TRACZYK, T., 1965). The gentle slope of the whole area to the west favours the slow precipitation flow along the depressions between dunes. Thus the depression area is additionally divided by streams.

The eastern part of KNP covering 500 ha — the so-called region of Dziekanowska Depression — within the dunes of Dziekanów and Sieraków, was examined. These dunes form ridges and in the basins between the dunes there are moorlands. The gruds are slightly above the moorland. The sands of the substrate come to the surface on dune zones and in the zone of gruds. On the remaining area they are covered with a humus layer. Thus we find there sandy soils of podzol type. The drains are in the lowest parts. Due to the impermeable ortstein layer and thin loamy layers the drains frequently overflow flooding the meadows and alder woods. In such depressions low peat moors are found (KOBENDZA 1930).

The level of ground waters is not very deep on the examined area, it is most frequently above 120 cm from the surface. The rhythm of seasonal fluctuations of ground water level has a similar course in various plant associations (TRACZYK, H., and TRACZYK, T., 1965). The differentiation of the area from the point of ground water level is illustrated in the diagram based on the data of TRACZYK, H., and TRACZYK, T. (Fig. 1). The zonal sequences in the diagram correspond to the plant succession suggested by these authors. According to these suggestions the succession starts from the most moist meadow communities — Caricetum elatae. In the region of streams this community in the course of drying is accompanied by the alder woods. Marginal parts of alder woods turn into oak-hornbeam

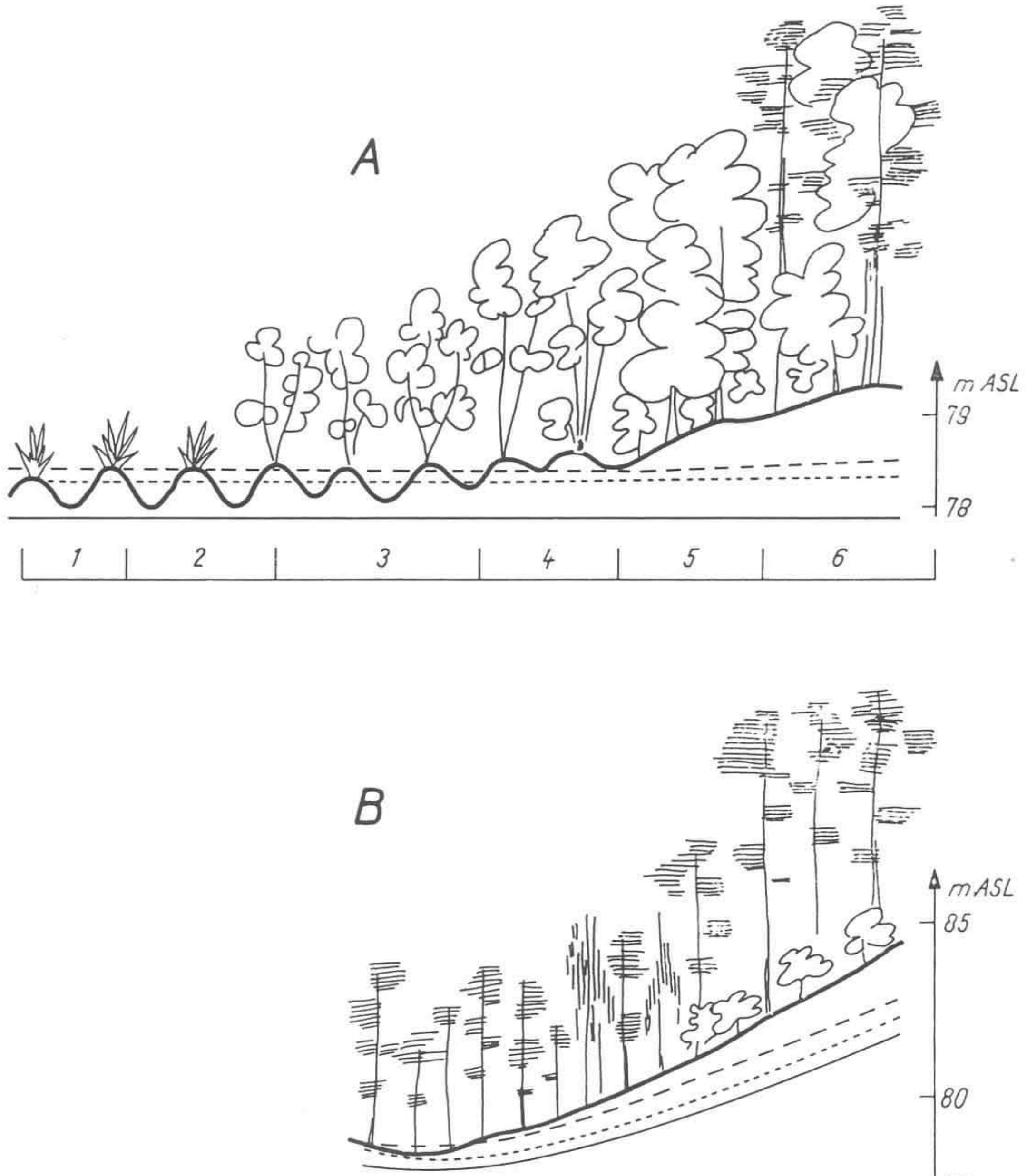

Fig. 1. The biotopes according to the natural succession (partly after H. and T. TRACZYK 1965)
Ground water level: -------- maximal, ... middle, ——— minimal
1 — Caricetum, 2 — Stellario Deschampsietum, 3 — Carici elongatae-Alnetum typicum, 4 — Carici elongatae-Alnetum deschampsietosum, 5 — Tilio carpinetum, 6 — Pino quercetum, 7 — Vaccinio uliginosi-Pinetum, 8 — pine forest, 9 — Vaccinio myrtilli-Pinetum

forests or in the case of drying of the top layer a mixed forest Pino-Quercetum is formed. The lower depressions with stagnant water are covered by Vaccinio myrtilli-Pinetum molinietosum and Vaccinio uliginosi-Pinetum. In conditions of the drying of ground these associations gradualy turn into associations of Vaccinio myrtilli-Pinetum.

2. Site and methods

The following meadow and forest communities (classification according to TRACZYK, H., and TRACZYK, T., 1965 and TRACZYK, T., 1966) were examined (compare Fig. 1):

(1) Caricetum elatae and Carici-Agrostetum caninae — mid-forest flooded meadows. They occur on muck bog soils. The thickness of humus horizon does not exceed 25 cm. It is formed by organic and mineral deluvial accumulation, strongly humified. From July until a late autumn there is noted no flooding. During observations in 1962 ground water table fluctuated in VII—VIII from + 12 to — 12 cm. pH (of soil) 5.3—6.0.

(2) Stellario-Deschampsietum — large damp pastures occupied "m~~u~~arsh" soils belonging to type of bog soils (MUSIEROWICZ 1958). The content of mineral components is low in these soils. The ground water table is high, but it seldom comes to the occurrence of water on the surface. During observations in 1962 VII—VIII it fluctuated from + 3 to — 30 cm. pH (of soil) 5.3—6.0.

(3) Carici elongatae-Alnetum typicum — flooded alder wood, almost all the year round only tufts at tree trunks are visible, occur on sedge-wooden peat soils with remnants of the wood *Alnus* and *Salix*. The ground water table from July is beneath the surface. During observations in 1962 VII—VIII it fluctuated from + 8 to — 4 cm.

(4) Carici elongatae-Alnetum deschampsietosum — drying up alder wood, flooded only for a short time, occur on slightly acid peat on sandy substrat. The ground water table is always beneath the surface. During observations 1962 VII—VIII it fluctuated from — 8 to — 25 cm. pH (of soil) 5.5.

(5) Tilio-Carpinetum — oak-hornbeam forest, an association found on higher areas both beside very damp alder woods and dry mixed forest, occur on brown soils with thick humus horizon

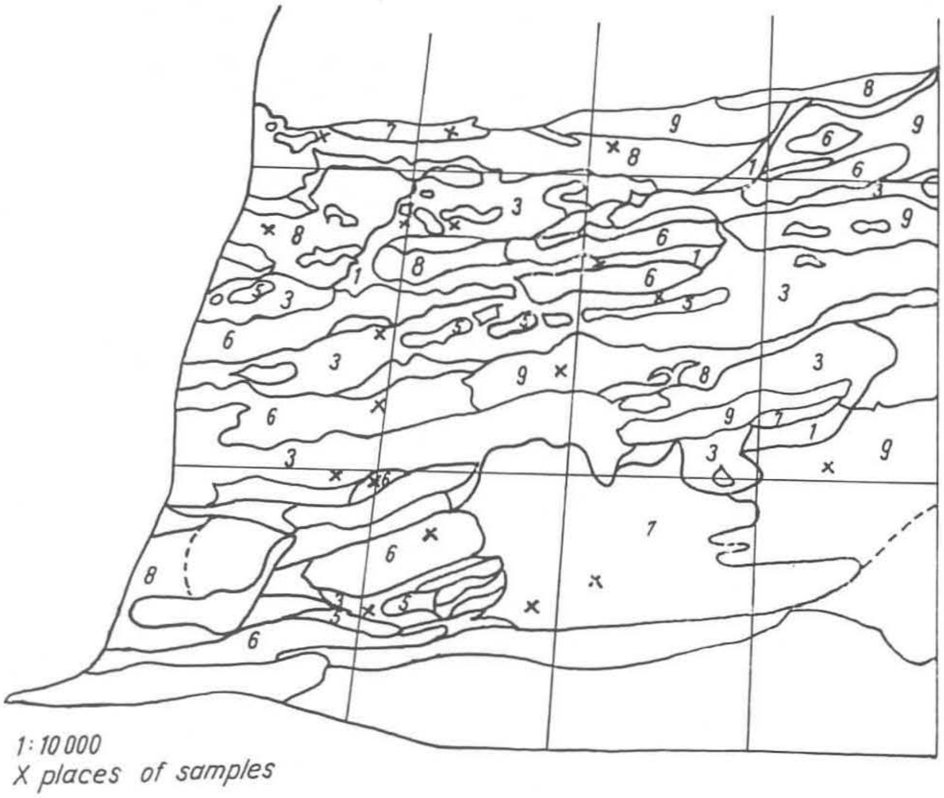

Fig. 2. Plant communities mosaic on part of the investigated area (after H. and T. TRACZYK 1965)
1—9 designations as in Fig. 1

(30–40 cm). The ground water table during observations in 1962 VII–VIII fluctuated from – 37 to – 58 cm. pH (of soil) 6.0–6.5.

(6) Pino-Quercetum – mixed forest on higher parts of gruds, occur on slightly podsoled podsol soils. Here was observed the deepest level of ground water. During observations in 1962 VII–VIII it fluctuated from – 72 to – 100 cm.

(7) Vaccinio uliginosi-Pinetum – pine swamp forest, occur on strongly podsoled and gleyed podsol soils. High ground water level fluctuated from – 5 to – 68 cm. During observations in 1962 VII–VIII it fluctuated from – 22 to – 47 cm. On the humus horizon there is a layer of slightly destroyed molder.

(8) Pine forest with an admixture of birch, transitory between humid and fresh pine forest.

(9) Vaccinio myrtilli-Pinetum (Pinetum muscinetum acc. to R. Kobendza) – fresh pine forest at the base of the dune occur on gleyed podsol soils. The ground water level fluctuated from + 2 to – 40 cm. During observations in 1962 VII–VIII it fluctuated from – 20 to – 40 cm.

All these plant communities form a complicated mosaic in the examined area (Fig. 2).

When elaborating the material the fauna from the communities 1 and 2, 3 and 4, 5 and 6, 7 to 9, was sometimes treated jointly and called the fauna of meadow, alder wood, mixed forest, pine forest biotopes, within which more humid and drier areas could be distinguished.

The Collembola material was sampled using a device cutting soil samples of a surface 10 cm^2 and 10 cm deep. The fauna was automatically released from the samples in a simplified apparatus of Tullgren type (description and functioning of the apparatus of M. Kaczmarek 1963).

Samples representing particular biotopes were taken from various, sometimes even remote, stations (this was due to the mosaix character of the area), 10 samples from each station. This was an attempt to obtain a characteristic fauna of a determined biotope independently from the effect of microdifferentiation of the area (Table 1).

Table 1 Number of samples and individuals

Biotopes plant communities[1]	Meadows		Alder woods		Mixed woods			Pine woods		total
	1	2	3	4	5	6	7	8	9	
1960										
Samples	65[2]	60	40	50	40	50	70	60	60	495
individuals	1028	1284	838	273	899	1243	909	940	1177	8597
1962										
Samples	50	50	40	50	40	50	60	60	60	460
individuals	511	461	503	2040	985	2250	1613	1337	1360	11060
Total										
samples	115	110	80	100	80	100	130	120	120	955
individuals	1539	1745	1341	2313	1884	3499	2522	2277	2537	19657

in both years the samples were taken in July and August

1) compare with Fig. 1

2) 5 additional samples

Similarity of species composition of egzamined biotopes was determined by index $P = \frac{c}{a + b - 2c}$ where: a = number of species of biotop A, b = number of species of biotop B, c = number of mutual species.

To avoid confusion when estimating the changes in density of Collembola as their seasonal abundance fluctuations are quite considerable (data for the KNP area cf. M. Kaczmarek 1963), all the samples were taken in July and some in August. To complete the data on the range of density fluctuations in particular biotopes and the differences in species composition, the samples were taken for the second time in the same place and data after two years, when the ground water level in KNP was much higher.

This material provided tests of Collembola reaction to varying moisture in the biotope: (a) in the biotopes according to natural succession from damp mid-forest meadows to mixed forest, and from swamp forest to fresh forest, (b) within each biotope on drier and more moist areas (flooded meadows and only swamp meadows, alder woods flooded for a longer time and drying up alder woods, oak-hornbeam forest beside alder woods and mixed forest etc.), (c) at changes in moisture in the same period but in different years (July, August 1960 and 1962).

3. Results

3.1. Occurrence of Collembola species on the examined area

The material contains 98 species (the list in Tab. 2—5 contains 9 species extra, which were found on the examined area but at a different time). 17 species are common for the examined area. The list of Collembola fauna of the Mazowiecka Lowland (Stach 1964) does not include 52 species from our list. Among them 3 species are new to Polish fauna: *Folsomia fimetarioides* mass occurrence on the whole area (hitherto known in Baltic countries). *Neanura tetrophthalma* found once as the only specimen (species found from Ural to west Germany; Dunger 1966). *Orchesella albofasciata* found on the examined area only on meadows, previously found on Podole (Ukraina). The species found in pine forests, the genus of which is difficult to determine, will be separately described and in the list is indicated as Collembola gen. sp. Beside this exception the systematic nomenclature is according to the catalogue of Polish fauna for Apterygota (Stach 1964).

The division of Collembola into ecological groups is made according to the depth of occurrence in soil, which affects the pigmentation, length of limbs, way of sampling food (Gisin 1943, Bockemühl 1956). The following groups are distinguished: (1) eudaphon, (2) hemiedaphon, (3) atmobios.

Our sampling technique provides mainly material composed of species belonging to eu- and hemiedaphon. The third group is being partly caught and the rare species are probably omitted. Of course, the division into groups is agreed upon: young individuals of atmobios should according to the listed requirements belong to hemiedaphon, and the

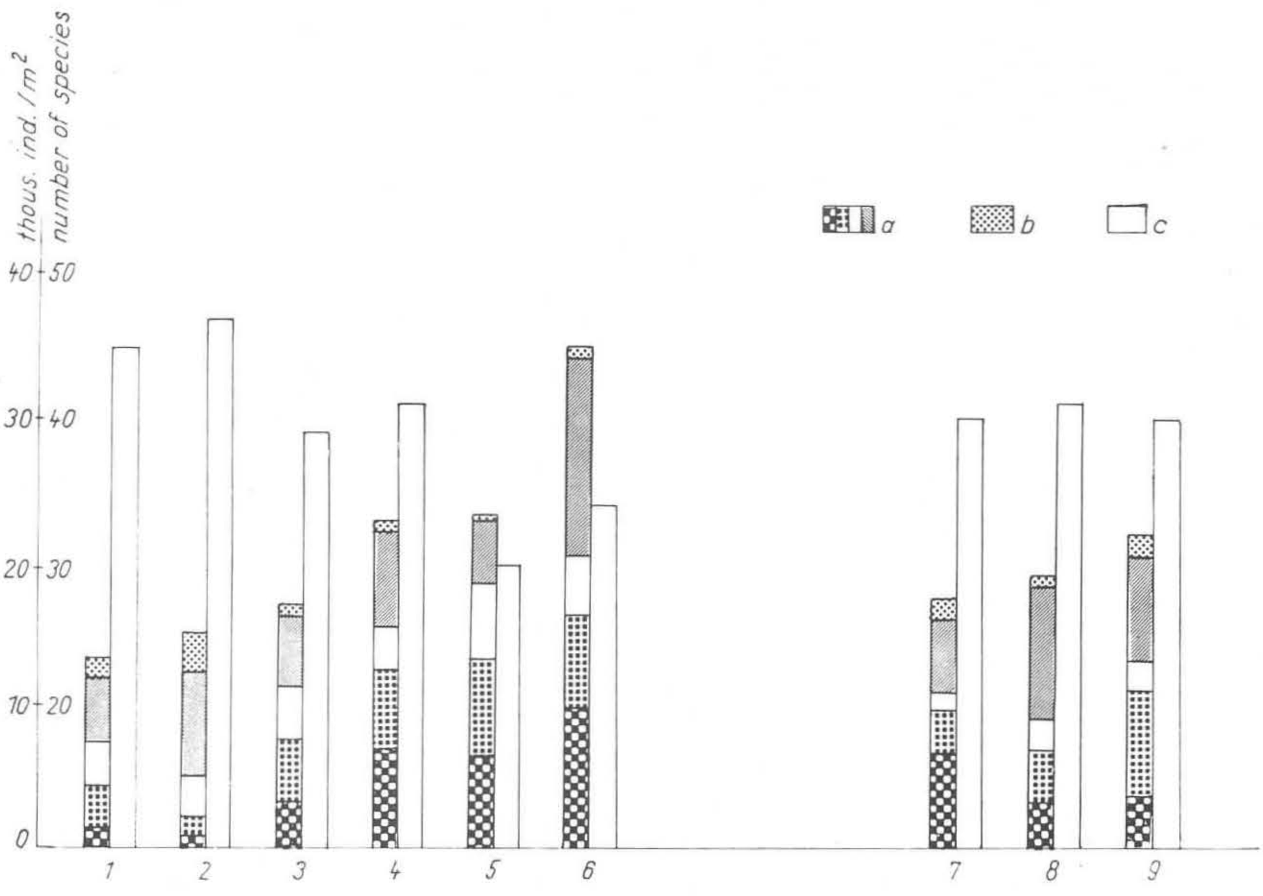

Fig. 3. Collembola in the examined biotopes
1—9 designations as in Fig. 1
a — ubiquists density (from the left — *Folsomia fimetarioides*, *Folsomia quadrioculata*, *Isotomiella minor*, the other ubiquist species), b — specific species density, c — number of species

young individuals from hemiedaphon would be frequently ascribed to eudaphon. Discussing the material we assume that to eudaphon belong species from the genera *Onychiurus*, *Tullbergia*, *Anurida*, *Willemia*, partly *Folsomia*, *Proisotoma*, *Isotomiella*, *Neelus*, *Megalothorax*, *Arrhopalites;* to hemiedaphon: *Neanura*, *Pseudachorutes*, *Friesea*, *Xenylla*, *Hypogastrura*, *Podura*, partly *Folsomia*, *Ballistura*, *Vertagopus*, *Isotoma*, *Isotomurus*,

Table 2 Species found in one biotop only (figures — density classes)

	Species	Meadows	Alder woods	Mixed woods	Pine woods
o	*Odontella lamellifera* (Axels.)	1			
o	*Folsomides parvulus* Stach	1			
o	*Ballistura crassicauda* (Tullb.)	1			
o	*Isotoma hiemalis* Schött	1			
	Isotomurus palustroides subciliatus Stach	2[1]			
v	*Entomobrya multifasciata* (Tullb.)	1			
	Entomobrya corticalis (Nic.)	1			
	Orchesella cincta (L.)	1			
ox	*Orchesella albofasciata* Stach	3			
o	*Arrhopalites principalis* Stach	1			
	Heterosminthurus linnaniemi (Stach)	1			
	Heterosminthurus novemlineatus (Tullb.)	1			
	Sminthurus flaviceps Tullb.	1			
oxv	*Neanura tetrophthalma* (Stach)		1		
o	*Xenylla schillei* Börn.		1		
o	*Isotomina thermophila* (Axels.)		1		
v	*Orchesella bifasciata* f. *nigra* Stach		1		
o	*Sminthurides malmgreni* (Tullb.)		1		
	Sminthurides aquaticus (Bourl.)		1		
o	*Deuterosminthurus bicinctus* (Koch)		1		
	Allacma fusca (L.)		1		
o	*Arrhopalites pygmaeus* (Wank.)		1		
	Pseudachorutes dubius Krausb.			1	
v	*Sinella myrmecophila* (Reut.)			1	
v	*Entomobrya arborea* (Tullb.)			1	
o	*Dicyrtoma fusca* (Luc.)			1	
ov	*Orchesella pseudobifasciata* Stach			1	
o	*Xenylla brevisimilis* Stach				5[1]
	Xenylla sp.				1
ov	*Isotomurus alticolus* (Carl)				1
	Willowsia buski (Lubbock)				1
	Entomobrya quinquelineata Börn.				1
	Orchesella spectabilis Tullb.				1
ov	*Orchesella xerothermica* Stach				1
	Orchesella bifasciata Nic.				1
o	*Orchesella multifasciata* Scherb.				1
ov	Gen. sp. indet.				1

Note — designations on the border
o — species new for Mazowiecka Lowland
x — species new for Poland
v — species found in other investigations in this biotop
Density classes: 1 — 1 to 2 individuals per 1 dcm^2
2 — 2 to 4 individuals per 1 dcm^2
3 — 4 to 6 individuals per 1 dcm^2
4 — 6 to 8 individuals per 1 dcm^2
5 — 8 to 10 individuals per 1 dcm^2
6 — 10 to 20 individuals per 1 dcm^2
7 — more then 20 individuals per 1 dcm^2

[1] the high number is the consequence of individual aggregation.

Table 3 Species with preference for particular biotopes (designations as in Table 2) figures — density classes

Species	Biotopes Plant communities	Meadows		Alder woods		Mixed woods		Pine woods		
		1	2	3	4	5	6	7	8	9
0	*Folsomia fimetaria* (L.)	**5**	**3**	1	1	1	2	1	1	1
0	*Lepidocyrtus ruber* (Schoett.)	**5**	**6**	1						
	Lepidocyrtus cyaneus Tullb.	**2**	**4**	1	1		1		1	
	Ballistura schoetti (D. T.)		**2**					1		
	Isotomurus palustris (Müll.)	**4**	**2**	**4**	**3**					
	Isotoma viridis Bourl.	**2**	**6**	**2**	**2**	1	1	1	1	1
0	*Podura aquatica* L.	**1**		**1**	**1**					
	Isotoma olivacea Tullb.			**1**	**3**	1	1	1	1	1
0	*Onychiurus granulosus* Stach	1	1	2	**5**	2	**4**	**3**	**5**	**5**
	Tomocerus flavescens (Tullb.)	3	1	**4**	3	2	3	**4**	**4**	2
	Hypogastrura armata (Nic.)	1	2	2	**5**	**4**	**4**	**4**	**3**	2
0	*Anurophorus laricis* Nic.					**2**	**3**	**4**		
0	*Friesea mirabilis* (Tullb.)	2	2	2	2	2	**3**	**4**	**6**	**4**
	Orchesella flavescens (Bourl.)	1		2	2	1	2	**6**	**4**	2
	Isotoma violacea Tullb.	1	1	1	1			**3**	1	1
0	*Onychiurus absoloni* (Boern)				1	1	1	**2**	1	1
0	*Proisotoma minima* (Abs.)	1	1	1			1	1	1	**5**

Table 4 Species from Different biotopes found as single individuals (designations as in Table 2)

	Species/Biotopes	Meadows	Alder woods	Mixed woods	Pine woods
0	*Entomobrya muscorum* (Nic.)	×	×	×	×
0	*Anurida granaria* (Nic.)	×	×	×	×
0	*Anurida pygmaea* Börn.	×	×	×	×
0	*Willemia anophthalma* Börn.	×	×	×	×
	Neanura muscorum (Templ.)	×	×	×	×
0	*Megalothorax minimus* Will.	×	×	×	×
0	*Sminthurinus aureus* (Lubb.)	×	×	×	×
	Sphyrotheca lubbocki (Tullb.)	×	×	×	×
0	*Willemia aspinata* Stach		×	×	×
	Sminthurus viridis (L.)		×	×	×
0	*Anurida anophthalmica* Stach			×	×
0	*Hypogastrura socialis* (Uzel)			×	×
	Entomobrya nivalis (L.)	×			×
0	*Entomobrya marginata* (Tullb.)	×			×
0	*Isotomina bipunctata* (Axels.)	×			×
	Proisotoma sp.	×			×
0	*Brachystomella parvula* (Schäff.)	×			×
0	*Anurida granulata* Stach	×			×
0	*Hypogastrura manubrialis* (Tullb.)	×			×
0	*Sminthurides pseudassimilis* Stach	×			×
	Deuterosminthurus repandus (Ågren)	×			×
	Heterosminthurus bilineatus (Bourl.)	×		×	×
0	*Sphaeridia pumilis* (Krausb.)	×		×	×
	Ptenothrix leucostrigata Stach	×		×	×
0	*Neelus murinus* Fols.	×	×		×
0	*Sminthurides schoetti* (Axels.)	×	×		×
0	*Sminthurus marginatus* Schött.	×	×		×
0	*Dicyrtomina minuta* (O. Fabr.)	×	×		×
	Tomocerus minutus (Tullb.)		×		×
	Tomocerus vulgaris (Tullb.)		×		×
0	*Pseudachorutes subcrassus* Tullb.		×		×
	Vertagopus cinerea (Nic.)		×		×
0	*Sminthurinus niger* (Lubb.)		×		×
0	*Stenacidia violacea* (Reut.)		×		×
	Tomocerus longicornis (Müll.)		×	×	
0	*Schoettella inermis* (Tullb.)			×	×
	Ptenothrix atra (L.)			×	×

Lepidocyrtus, *Willowsia*, *Sinella*; to atmobios: *Tomocerus*, *Entomobrya*, *Orchesella* and all species from the group Symphypleona apart from the already mentioned ones.

In the examined biotopes according to natural succession from meadows to mixed forest the number of Collembola species decreases (Fig. 3). Simultaneously, in more humid plant communities of each biotope the number of species is smaller than in the drier ones. The relations in pine woods are different. In all communities the number of species is nearly equal there.

Among the species we may distinguish groups differing as to their occurence: species found only in one biotope (Table 2), in few biotopes or in all biotopes with preference to some (Table 3), species found in various biotopes in very small amounts (Table 4), and a group of species found everywhere and abundantly (Table 5). Species found in only one biotope belong usually to atmobios. A number of such species together with species preferring the given biotope illustrate the species specificity, which gradually decreases according to natural succession of biotopes. (On meadows total 20 species, alder woods — 16, mixed woods — 9, pine woods — 19; Table 2 and 3.) Some species prefer in general forest areas and these are: *Onychiurus granulosus*, *Hypogastrura armata*, *Tomocerus flavescens*, or exclusively pine forests: *Onychiurus absoloni*, *Isotoma violacea*, *Proisotoma minima*, *Orchesella flavescens*, or very moist areas: *Podura aquatica*, *Folsomia fimetaria*, *Ballistura schoetti*, *Isotoma viridis*, *Isotoma olivacea*, *Isotomurus palustris*, *Lepidocyrtus ruber*, *Lepidocyrtus cyaneus*, or mixed and pine forest: *Friesea mirabilis*, *Anurophorus laricis*.

Table 5 Ubiquist species with high density in all biotopes (designations as in Table 2) figures — density classes

Species	Plant communities:	1	2	3	4	5	6	7	8	9
ox	*Folsomia fimetarioides* (AXELS.)	6	4	7	7	7	7	7	7	7
	Isotomiella minor (SCHÄFF.)	7	7	7	7	7	7	6	7	7
	Folsomia quadrioculata (TULLB.)	7	6	7	7	7	7	7	7	7
	Isotoma notabilis SCHÄFF.	5	5	4	6	4	6	6	6	5
	Lepidocyrtus lanuginosus (GMEL.)	4	5	2	5	6	7	6	6	6
	Onychiurus armatus (TULLB.), STACH	3	6	5	6	6	7	3	5	5
	Tullbergia krausbaueri (BÖRN.)	1	3	2	1	3	3	3	6	2

Table 6 The coefficient of biotopes similarity

Biotopes	Meadows		Alder woods		Mixed woods		Pine woods		
Total No. of species	47	45	39	41	30	34	40	41	40
Plant communities	2	1	3	4	5	6	7	8	9
2		**1,1**	0,8	0.5	0,5	0.7	0,8	0,6	0.7
1			**1,4**	0,8	0.9	**1,2**	**1,0**	**1,1**	0.8
3				**1,0**	0,9	**1,1**	**1,0**	0.4	0.7
4					**1,0**	**1,1**	0,8	**1,0**	0,6
5						**2,7**	**2,0**	**1,4**	0,9
6							**1,8**	**1,5**	**1,4**
7								**1,3**	**1,0**
8									0,9
9									—

The index of similarity of species composition of the examined biotopes shows a great similarity of all biotopes. A more individual species composition have only the fresh pine forest and large damp pastures (Table 6).

3.2. Density of Collembola

On the examined area the density of Collembola reaches 45000 ind./m^2 (Pino-Quercetum in the more humid year of studies). In the gradient of biotopes from meadows (12,000 – 14,000 per 1 m^2) through alder woods (16000 – 22000 per 1 m^2) to mixed forests (23,000 – 24,000 per 1 m^2) the density constantly increases. In the gradient of gradually drier pine forests it also increases but less so — from 17000 to 21000 per 1 m^2 (Fig. 3). This is first of all the result of increase in the number of ubiquists — *Onychiurus armatus*, *Folsomia fimetaroides*, *Folsomia quadrioculata*, *Isotomiella minor*, *Lepidocyrtus lanuginosus* (Fig. 3). In general the number of ubiquists is in all biotopes more than 83 % of the total number.

Changes in the total number of Collembola due to variable conditions at the same time but in different years, show in the more humid year a decrease in density on especially moist areas, where the flood waters disappeared at the end of July (wet alder woods and meadows), and an increase in number on all other areas, where spring water flooding was shorter (drying up alder wood, swamp wood: Fig. 4).

In all biotopes the proportions of particular ecological groups are very similar. On the average these relations are as following — 56,5 % of eudaphon, 38,7 % of hemiedaphon, 4.9 % of atmobios (Fig. 5). In a more humid year of studies the density in mentioned ecological groups undergoes various changes in different biotopes. The density of eu- and hemiedaphon in more moist biotopes — on both meadow types and the flooded alder wood — decreased. In the drier alder wood the density of eu- and hemiedaphon considerably increased, whereas in mixed forests only the eudaphon density increased. In pine forests the increase in eu- and hemiedaphon density took place everywhere, and was the highest in swamp woods. The density of atmobios was in both years not very

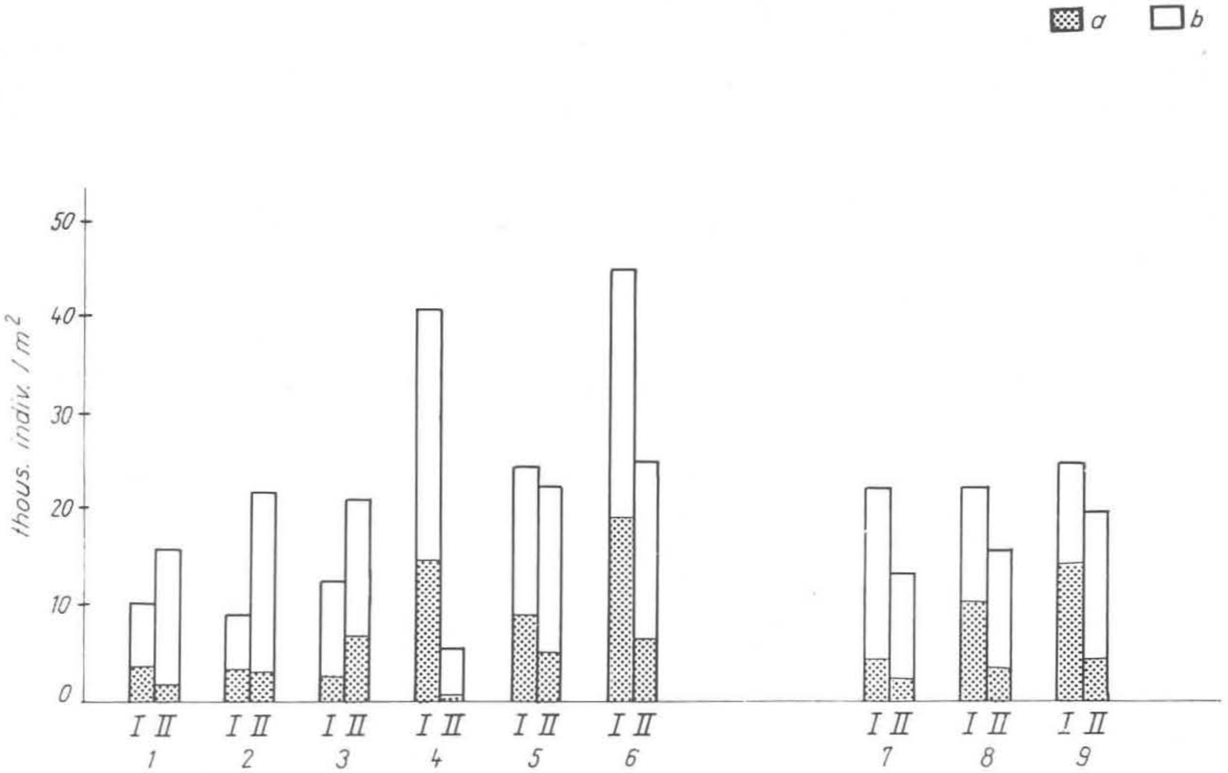

Fig. 4. Collembola density in biotopes in "wet" and "dry" years
1 – 9 designations as in Fig. 1
I — "wet" year, II — "dry" year
a — juv. individuals, b — adult individuals

high, but it increased visibly in the more humid year in swamp wood and pine forest of a transitory character.

Density of juvenile forms (measuring less than $^2/_3$ of an adult individual) and their share increase gradually from mid-forest meadows to mixed forests and in the row of gradually drier pine forests. In the humid year the density of juvenile forms increased in all biotopes with the exception of flooded alder wood, and the greatest increase was observed on the driest areas. Thus we may conclude that greater humidity favours greater reproduction and survival of juvenile forms, or the reproduction period begins later.

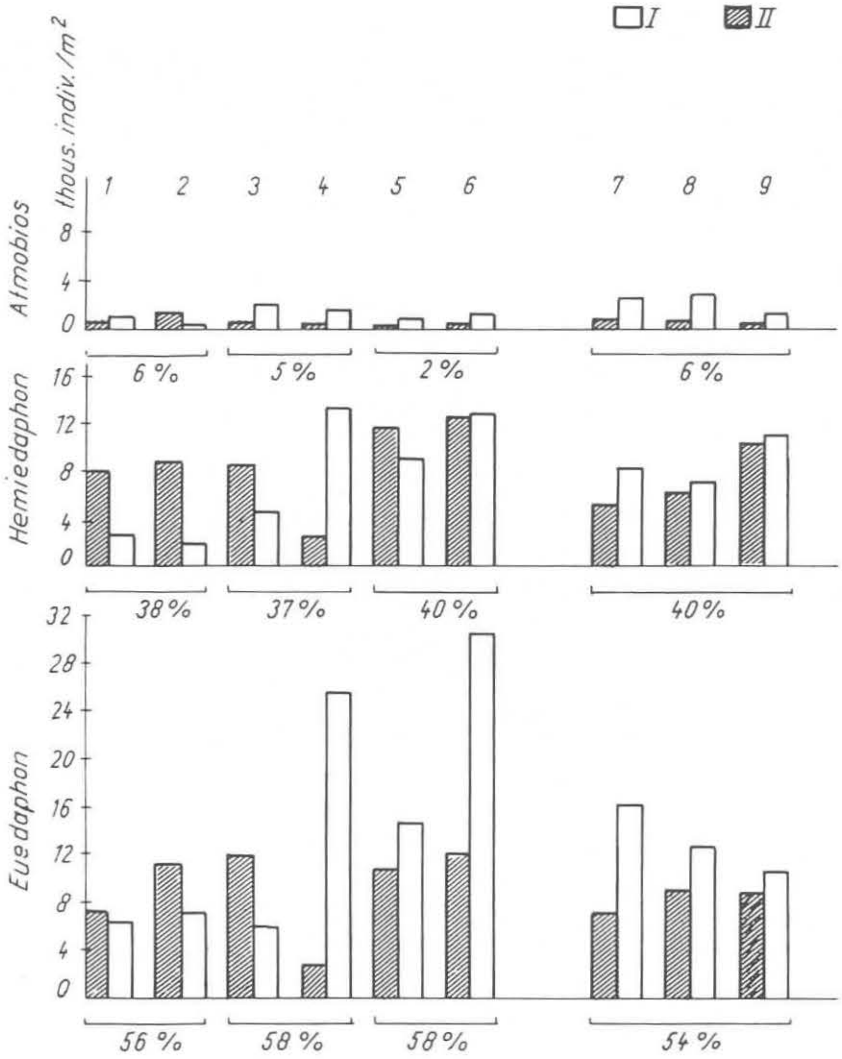

Fig. 5. Ecological groups of Collembola
1–9 designations as in Fig. 1
I, II – designations as in Fig. 4

3.3. Frequency of Collembola

The extent of covering the examined area by the Collembola population (frequency) was calculated using the per cent of "full" samples (with some individuals) in the total number of samples, and it was found to range in different biotopes from 78 to 100%.

The frequency of ubiquists against the examined biotopes according to the natural succession shows their connection with the examined areas. The frequency of species *Folsomia fimetarioides*, *F. quadrioculata*, *Onychiurus armatus* increases when passing into forest areas and remains there on a similar level. In species *Lepidocyrtus lanuginosus*, *Tullbergia krausbaueri* the area covered is much higher in drier biotopes – in mixed and pine forests. In species *Friesea mirabilis* the covered area is much greater only in pine forests as compared with other biotopes. The area covered by such species as *Isotomiella minor*, *Isotoma notabilis*, *Hypogastrura armata* is on a similar level in meadow and forest biotopes (Fig. 7).

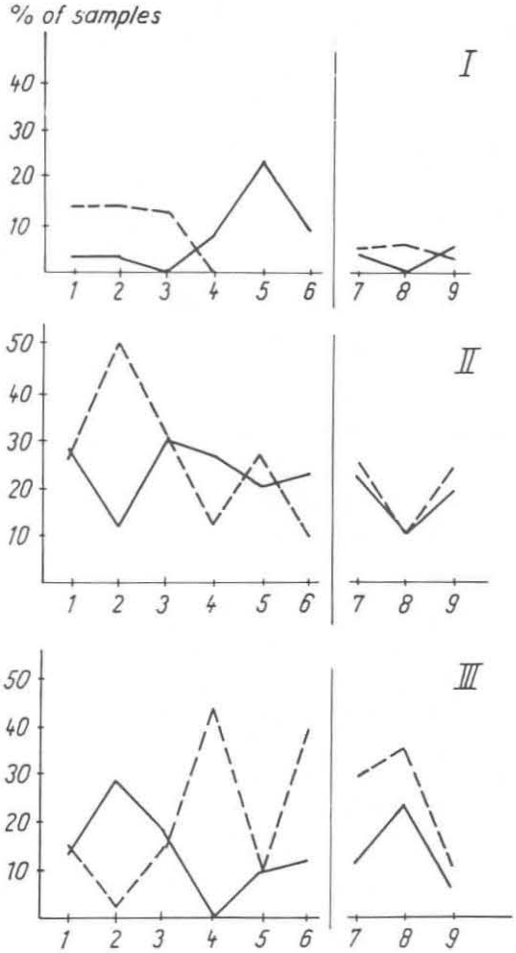

Fig. 6. Territorial coexistence of species
- - - - "wet" year, ——— "dry" year
1–9 designations as in Fig. 1
I – % samples without any species, II – % samples with 1 and 2 species, III – % samples with 8 and more species

In the humid year the total frequency of Collembola was lower in more moist biotopes and in the drier year – in drier biotopes (Fig. 6^{I}). In the examined pine forests in both years the covering of the area by the Collembola population was similar on all areas. These changes illustrate the population adaptation (patchy occurrence of Collembola) at the periodically occurring unfavourable conditions – flooding of moist areas, drying up of higher situated areas.

In the drier year, when the moist areas are flooded, the share of samples with 8 or more species simultaneously on pastures increases. At the same time the share of such samples decreases in the drier alder wood and dry mixed forest. The share of samples with 1–2 species decreases on meadows and increases in drier alder wood and in drier mixed forests. In other biotopes the shares of samples both with many species and with 1–2 species do not change from year to year almost at all. This, as it seems, proves that on drier areas of particular biotopes the spatial concentration of Collembola population displays much greater variations than on more moist areas (Fig. $6^{\mathrm{II,\ III}}$).

The spatial occupation of the area by particular species changes from year to year. In the more humid year the area occupied by species typical for moist areas — *Isotomurus palustris*, *Lepidocyrtus ruber*, *Lepidocyrtus cyaneus* — decreased to a considerable extent (probably due to flooding). The surface occuped by species typical for drier biotopes — *Friesea mirabilis*, *Lepidocyrtus lanuginosus* — frequently remained unchanged independently of the changes in number. The surface dominated by species abundantly found everywhere — *Onychiurus armatus*, *Hypogastrura armata*, *Folsomia quadrioculata*, *F. fime-*

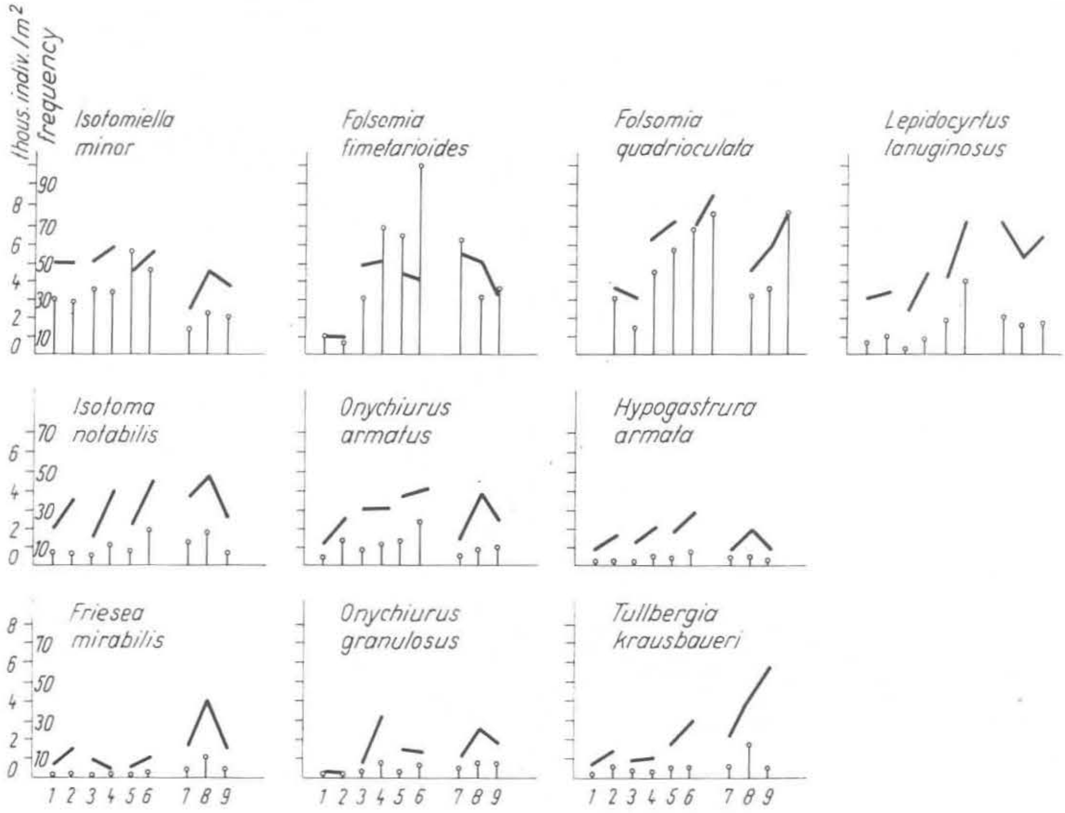

Fig. 7. Density and frequency of same ubiquist species; 1—9 designations as in Fig. 1
——— density, ——— frequency

Table 7 Changes in frequency and density of Collembola from "dry" to "wet" years

Species/Plant communities	1	2	3	4	5	6	7	8	9
Lepidocyrtus cyaneus	d	d	d						
Isotomurus palustris	d	d	d	i					
Lepidocyrtus ruber	d	d	—						
Folsomia quadrioculata	d	d	d	i	x	/	w	w	—
Isotomiella minor	d	—	d	i	i	i	—	—	i
Friesea mirabilis	—	d	—	i	d	w	i	—	—
Lepidocyrtus lanuginosus	—	d	d	i	w	/	—	d	—
Isotoma viridis	w	d	/	i	w				
Tullbergia krausbaueri	w	d	d	i	—	d	x	d	x
Onychiurus granulosus			/	i	w	/	x	i	i
Isotoma notabilis	/	d	d	i	i	i	i	i	i
Folsomia fimetarioides	i	i	d	i	i	i	i	i	x
Onychiurus armatus	i	i	/	i	i	i	i	i	x
Orchesella flavescens	i		i	i	i	i	i	i	i
Tomocerus flavescens	i		i	i	i	i	i	i	i

i — increase of frequency and density
d — decrease of frequency and density
— the frequency remains stable, the density changes
/ the density remains stable, the frequency changes
x the reverse changes of frequency and density

tarioides, Isotomiella minor, Isotoma notabilis, Lepidocyrtus lanuginosus — decreased in the humid year on the most moist areas — on meadows and damp alder wood. On the remaining areas the frequency of these species did not change or slightly increased. The area with species less closely connected with the soil and belonging to the atmobios group — *Tomocerus flavescens, Orchesella flavescens* — was greater everywhere in the more humid year. This is probably due to greater humidity in the ground air layer inhabited by these species (Table 7).

3.4. Density and frequency

The frequency of each one of the abundant species in different biotopes is most frequently proportional to its density in these biotopes. Within the same biotope on drier and more moist areas these two indices are also almost always consistent. The frequency proportions of various species in the same biotope do not illustrate the numerical relations between these species (Fig. 7). Thus, to compare the density of various species the knowledge of their frequency is insufficient. It is especially visible on the example of species *Lepidocyrtus lanuginosus* and *Folsomia fimetarioides* in pine forests. The specific conditions there favoured the high frequency of the species *L. lanuginosus* independently of its density, but did not favour the species *F. fimetarioides*. This allows to assume that the discussed species form a population having in different biotopes varying tolerance range to environmental conditions (Agrell 1941).

Changes of frequency as compared with changes of density in the both years of studies on particular areas (Table 7) show that most frequently the density and frequency change in the same direction and at density increase the frequency also increases, i. e. the species spreads. However, it happens that the frequency is more constant than the density. Then, at the change of conditions changes in density take place at constant frequency, i. e., at density increase the concentration of Collembola on space unit increase or at density decrease the population dispersion increases. Discordances of the direction of changes in frequency and density more frequently than in other biotopes, take place also in pine forests. It can be assumed that the connections between frequency and density in pine forests are different than in the other biotopes of the examined area. It can be also indicated that in species *Friesea mirabilis, Isotomiella minor, Lepidocyrtus lanuginosus* more frequently than in other species, the frequency remains on the same level at changed conditions (Table 7).

4. Discussion of results

Despite there were found 98 species, the taxonomic composition of Collembola communities from mid-forest meadows to mixed and pine forests changed rather slightly. The index of species similarity of distinguished biotopes was very high 0,4—2,7 (Table 6). This proves that the biotope specialization of Collembola is very small, especially within the forest biotopes, but it can be also due to the markedly mosaic character of the examined area — plant patches representing various succession stages are thickly interwoven (Fig. 2).

The list of species found only in one of the mentioned biotopes is rather conspicuous (Table 2). The smallest number of characteristic species is found in mixed forests with the most complex vegetation cover. This list may be completed by three species found only on meadows and in alder woods (*Podura aquatica, Isotomurus palustris, Lepidocyrtus ruber*), which are probably connected with the flooded areas, and by four species found only in associations of mixed and pine forests (*Anurida anophthalmica, Schoettella inermis, Anurophorus laricis, Ptenothrix atra*) probably connected with the pine. Besides, as many as 10 species have been simultaneously found pine forest (Table 3, 4). Probably such distribution is determined by the great accumulation of raw humus, which is common to these biotopes.

The majority of above mentioned species, however, were caught in extremely small numbers, so small that they could not have much significance for the ecology of examined communities (*Entomobrya corticalis* is found there rather occasionaly only on the meadows). In slightly greater numbers were caught: *Orchesella albofasciata* (10 ind./dcm^3) on meadows, *Isotomurus palustris* (about 3 ind./dcm^2), *Lepidocyrtus ruber* (about 5 ind./dcm^2) and *Podura aquatica* (about 1 ind./dcm^2) on flooded areas, and *Anurophorus laricis* (about 4 ind./dcm^2) in some wood associations. But not one of these 5 mentioned species dominated quantitatively even in the best conditions.

In all examined biotopes 17 species without special biotope preferences were the majority of studied communities. All the dominants (more than 1000 ind./m^2) were without any exceptions the undisputable ubiquists — very abundant in all biotopes (Table 5). Species found everywhere or in many biotopes, but with preference to a determined biotope or group were the subdominants (Table 3). This confirms the regularity about the dominant significance of less specialized species, observed previously in the studies on soil macrofauna of pine forest of Kampinos National Park (W. KACZMAREK 1963).

The observed repeatability of the community of dominants through all the examined biotopes makes much easier the analysis of general quantitative changes of Collembola community during the biotope succession. The history of the community in its general quantitative aspect is a comprehensive history of these few ubiquitous species. The taxonomic dissimilarities do not complicate the interpretation.

In the examined biotops distinguished according to natural succession from flooded meadows to wood communities, characterized by gradually decreasing ground water level, the total Collembola number increased gradually from 12000 to 24000 per 1 m^2. Also, within particular biotopes the density was higher on drier areas (Fig. 3). This is connected with the known phenomenon of greater density of soil mesofauna on areas less abundant in humus and with more sandy soil (GHILAROV 1965, NAGLITSCH 1963)[1]). It corresponds also with results of VANNIER (1970), that the higher is the soil humidity, the lower is the number of soil inhabiting animals. In both instances the share of juvenile individuals also increased (Fig. 4), which seems to point to the fact that greater survivoralship of juvenile forms was the source of observed increase in density.

However, a comparison of quantitative relations in years with a low and high level of ground waters, shows that the observed changes in density were not a simple function of biotope moisture. Although in the more humid year a decrease in the density of Collembola and share of juvenile individuals decreased, but only on the lowest flooded areas (wet meadows, flooded alder woods). On other areas both the total Collembola density and the share of juvenile individuals, and also the frequency (percentage of biotope territory inhabited by Collembola) were higher in the more humid year. The species distribution measured by the share of samples with 1—2 species and samples with a great number of species (more than 7), is worth paying attention. These shares (frequency) on more moist areas of the examined biotopes differ only slightly in both years. But on drier areas they underwent characteristic changes in the year with a higher level of ground waters. On meadows and in alder woods in the more humid year the share of samples with 1—2 species increased, whereas the share of samples with a great number of species decreased. In wood biotopes the high level of ground waters produced an opposite effect — the share of samples with 1—2 species decreased, and of samples with many species increased (Fig. 6). And so, due to increased substrate moisture not only the density of Collembola population increased, but also the possibilities of coexistence of many species (interspecific tolerance of cooccurrence).

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[1]) Studies on the proportion of density and number of Collembola species on lucerne fields growing in varying soil conditions showed that the density increases from heavy soils to sandy ones, and the number of species in this succession decreases. An analysis of soil porosity allowed to correlate the density of Collembola with the total space between soil particles filled with air (NAGLITSCH 1963).

The proportions of eu- and hemiedaphon were approximately the same in all examined biotopes and periods (Fig. 5).

All this points to the fact that the increase of Collembola density in the examined biotops distinguished according to natural succession is connected with the soil-forming process itself, which is a result of drying the area and plant succession and not directly of the soil moisture. Excessive moisture is a factor limiting the density of Collembola only in flooded biotopes. In other biotopes the moisture increase stimulates the population development and the range of its spatial occurrence, and also, as it seems, weakens the interspecific competition among the components of the community.

Against this background the differences in species abundance of Collembola communities in the examined biotopes are characteristic. The number of species in this series decreases, and simultaneously the share of ubiquists observed in all biotopes and areas increases (Table 3). This regularity in the light of general ecological theses on the relation between the population density and share of non-specialized species and the community differentiation (THIENEMANN 1925, W. KACZMAREK 1963) suggests gradual standarization of conditions of soil habitat in the examined biotope series. This regularity as used in our materials when comparing only various biotopes — types of associations and so meadows, alder woods, mixed and pine forests. Within each biotope the drier areas were represented by a higher number of species than on the more moist areas (Fig. 3). And so the increase in total Collembola density was accompanied here by greater number of species. This suprising regularity observed in a large majority of species was accompanied by a unanimity of changes in density and frequency (Fig. 7). Population density increase took place here among others by means of territorial spreading of the species occurrence in the biotope.

And so the above discussed inverse relation of density and number of species, found when comparing various biotopes, was commonly accompanied by a discordance in density and frequency in various species (Fig. 7). Thus the increase in density of particular species took place there not only by controlling new fragments of biotope, but by an increase of local concentrations. These two facts suggest the development of Collembola communities within each biotope separately (meadows, alder woods, mixed forests, pine forests) was much less affected by interspecific action than the changes in Collembola communities accompanying the "great" succession — meadows passing into alder woods, alder woods into mixed forest associations or meadows into pine forest associations. This is confirmed by the above discussed increased interspecific tolerance of Collembola from drier areas of each type of biotope under the influence of higher level of ground waters (increase of the share of samples with more than 7 species in each one).

5. Summary · Резюме

On the examined area of the Kampinos National Park, which is a mosaic of plant associations, four biotopes according to natural succession have been distinguished, on which the drier and more moist areas were examined for two years, 955 samples were taken, from which 19657 Collembola individuals belonging to 98 species (3 species new in Poland, 52 species found for the first time on the Mazowiecka Lowland) were extracted.

From mid-forest meadows to mixed forests and in the series of gradually drier pine forests the number of Collembola species gradually decreases. The species peculiarity of these biotopes also decreases. The ubiquists, which are more than 80% of the density of examined population determine the course of all observed quantitative phenomena.

The total Collembola density increases in the examined series of biotopes from 13,000 to 35,000 per 1 m², and in pine forests from 17000 to 22000 per 1 cm². On very damp areas opening

the succession in the year with a higher level of ground waters, a decrease in total Collembola density was observed, and also a limitation of their spatial occurrence (decline of frequency). The same conditions on drier areas (further succession stage) resulted in a considerable density increase and wider occurrence area (greater frequency). In all biotopes greater moisture in the second year of investigations affected the greater share of juvenile individuals in the population.

All these phenomena had an analogous course in the series of examined pine forests.

The presented results show that the changes recorded for the Collembola population are connected with the soil-forming process, which takes place in the course of drying of soil and plant succession, and are not directly due to the soil moisture régime.

Восточная часть Кампиноского Национального Парка, где велись исследования погохвосток, представляет собой мозаику растительных ассоциаций. Выделено сукцессионный ряд растительных сообществ, где собраны пробы отдельно с более сухих и влажных биотопов.

Из 955 проб, собранных в течение двух лет, извлечено 19657 особей погохвосток, принадлежащих к 98 видам. Найдено 3 вида новых для фауны Польши и 47 видов новых для Мазовецкой низменности.

Число видов погохвосток в исследованном сукцессионном ряду постепенно уменьшается. Уменьшается также видовая специфика выделенных биотопов. Убиквистические виды, составляющие более 80% численности исследованной популяции, определяют направление всех отмеченных количественных изменений.

Общая численность погохвосток возрастает в сукцессионном ряду от 13 до 35 тыс. на 1 м^2, а в сосновых лесах от 17 до 22 тыс. на 1 м^2. В самых влажных биотопах, представляющих собой начальные этапы сукцессии, для года с высоким уровнем грунтовых вод характерно снижение общей численности погохвосток и ограничение их пространственного распространения (снижение встречаемости). В том же году в более сухих биотопах произошло увеличение численности и расширение занятого погохвостками пространства (увеличение встречаемости). Во всех биотопах увеличение влажности повлияло на увеличение в популяции процента ювенильных форм. В сосновых лесах все описанные явления протекали таким же порядком.

Представленные результаты указывают, что изменения, отмеченные в популяции погохвосток, связаны с почвообразовательными процессами, которые происходят в результате подсыхания грунта и растительной сукцесси, а не непосредственно с изменением влажности почв.

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